

THE VERTEBRAE OF FOUR AUSTRALIAN ELAPID SNAKES (SQUAMATA: ELAPIDAE)

by MEREDITH J. SMITH*

Summary

SMITH, MEREDITH J. (1975).—The vertebrae of four Australian elapid snakes (Squamata: Elapidae). *Trans. R. Soc. S. Aust.* **99**(2), 71-84, 31 May, 1975.

In vertebral morphology, the elapid species *Pseudechis porphyriacus*, *Austrelaps superba*, *Notechis scutatus* and *Pseudonaja nuchalis* conform with general descriptions and closely resemble each other. Features not previously noted are that epizygapophysial spines appear on the first 8 to 10 vertebrae, and that bilaterally on every precloacal vertebra a foramen opens through the accessory process near the anterolateral edge of the prezygapophysial facet. No morphometric feature was found to completely separate any two genera, i.e. there was some overlap in the values of all the characters (ratios) studied. However, in general *P. porphyriacus* vertebrae are distinguished by their relatively long accessory processes, *A. superba* by their short accessory processes and lesser width across postzygapophyses, and *N. scutatus* by their greater width across postzygapophyses and shorter neural spines. *P. nuchalis* vertebrae have strong subcentral ridges.

Fossil vertebrae from a Pleistocene deposit differ from *P. porphyriacus*, *A. superba* and *N. scutatus* but resemble *Pseudonaja* in most features. The fossils differ from modern *P. nuchalis* chiefly in having a thicker zygosphenes and relatively wider postzygapophyses. As these are features which develop with increasing size of vertebrae, the fossil vertebrae are assigned to the genus *Pseudonaja*.

Introduction

Although snake vertebrae have been recorded from Australian Pleistocene deposits (Lydekker 1888, Merrilees 1968), the only species that has been identified is the Carpet Snake, *Morelia spilotes variegata* Gray (= *Python variegatus*) from Marmor Quarry, Queensland (Longman 1925). No detailed studies have been published of Australian snake vertebrae and the diagnostic characters have not been established. The need to determine the reptile fauna in a Pleistocene cave deposit stimulated the present study.

The sixty-odd Australian species of elapids have been arranged in 29 genera (Worrell 1963) or fewer (McDowell 1967, 1970), but only seven genera contain species with a recorded maximum length of over 0.9 m. As centrum lengths of some of the Pleistocene vertebrae suggested that the specimens from which they were derived must have exceeded 1.5 m, the 22 genera of smaller species (less than 0.9 m maximum length) have not been considered. Nor have *Demansia* [restricted to

the whip snakes by Worrell (1963)], *Hoplocephalus*, and *Oxyuranus* been examined as their range is northern and eastern Australia (Worrell 1963). Specimens have been studied from the remaining four genera, *Austrelaps*, *Notechis*, *Pseudechis* and *Pseudonaja*, which are each represented in southern Australia by one or more common species.

The exact column position of an isolated vertebra is impossible to determine (Johnson 1955) and in elapids, with well-developed hypapophyses on all pre-cloacal vertebrae, division of the pre-cloacal column into regions is virtually impossible. Nevertheless vertebral shape changes along the column, and to identify single vertebrae it is essential to know the range of variation within individuals and species. Auffenberg (1963) based his descriptions and diagnoses on middle pre-caudal vertebrae (determined as such by the relative size of the neural canal) and avoided considering intracolumnar variation. Although Johnson (1955) measured 10 precloacal vertebrae at regular intervals along the column, he assumed

* Department of Zoology, University of Adelaide, Adelaide, S. Aust. 5000.

equal variances (between specimens) of ratios of these measurements and in his comparisons he used only the mean for each specimen. Here, entire vertebral columns have been examined in an attempt to assess the morphological and morphometric variation which occurs within individuals and species, and to find unique specific characters. As most elapids have over 200 vertebrae, the available samples are large and the time required for detailed examination of one individual snake precludes sampling many individuals.

Because taxonomy of species of *Pseudonaja* and *Austrelaps* is confused (Rawlinson 1969, Storr 1964) comparisons are made at the generic rather than species level.

Materials and Methods

A total of 2,123 vertebrae from nine Recent specimens (Table 1) and 556 Pleistocene vertebrae were examined. Of the nine modern specimens, four specimens of *Pseudechis porphyriacus*, one *Pseudonaja nuchalis* (R14064) and one *Notechis scutatus* (R14059) were collected near Armidale, New South Wales; the one *Austrelaps superba* was collected at Uraidla, South Australia. The localities of one *P. nuchalis* (R14065) and one *N. scutatus* (R14058) are unknown.

The common brown snake, *Pseudonaja textilis* (Duméril & Bibron), has been described as a separate species from the western brown snake, *Pseudonaja nuchalis* Günther, but it is not yet clear (Storr 1964) whether they are distinct or are merely races of a single species, *P. textilis*. One clearcut diagnostic feature is the shape of the nasal bones, which are anteriorly concave on the lateral margins in *P. nuchalis* but anteriorly convex in *P. textilis* (Worrell 1963). In R14064 and R14065 the nasals are anteriorly concave and hence are attributable to *P. nuchalis*.

The cleaned skeletons were dried and completely disarticulated for study. The specimens are now lodged in the South Australian Museum, with register numbers as above.

The Pleistocene vertebrae were excavated from an extensive bone deposit in Victoria Cave, Naracoorte, South Australia. The age of this deposit is unknown, but the abundance of extinct marsupials and the absence of remains of aboriginal man suggest that the deposit accumulated during the Pleistocene but was sealed during Recent time. As the vertebrae were collected singly in many locations in the bone deposit, they probably represent

at least several individuals. Visual examination of the fossils revealed that 454 of them were similar to each other in shape, and distinctly different from the rest, which were of several kinds. The latter, heterogeneous group will be discussed in a later paper. Of the larger group of 454, the 80 most complete were examined in detail and measured in the same way as the modern vertebrae.

Because reptiles grow throughout their life, absolute dimensions of the vertebrae are of little use in comparing individuals or species. Ratios between dimensions have been calculated, the denominator being vertebra length in most comparisons. Mean values of ratios have been prepared independently for each individual snake, and are given as mean, \bar{x} , \pm standard error, followed in brackets by the number of vertebrae measured. The non-independence of measurements of different vertebrae of the one individual precludes statistical comparison of these samples (Siegel 1956).

From a preliminary study of numerous characters of snake vertebrae, characters were selected that vary between species within the family Elapidae, exhibit low intracolumnar variation and are well preserved in fossils. To establish variation throughout the column, every fifth vertebra was measured in two specimens of each of *P. porphyriacus*, *P. nuchalis* and *N. scutatus*, and one *A. superba*.

Descriptive techniques and terminology follow Auffenberg (1963). Measurements were made to 0.1 mm with dial calipers, as in Fig. 1:

- pr-po Length between zygapophyses—distance between most anterior point of prezygapophysis to most posterior point of postzygapophysis.
- ap-ap Width across accessory processes—distance between outermost tips of accessory processes.
- po-po Width across postzygapophyses—distance between outermost points of the postzygapophysial facets.
- prl Length of prezygapophysis—the longest diameter of the prezygapophysial facet (even though this was almost perpendicular to the long axis of the centrum).
- pr Width of prezygapophysis—the maximum diameter at right angles to the length of the prezygapophysis (the prezygapophysial width being almost parallel to the long axis of the centrum).

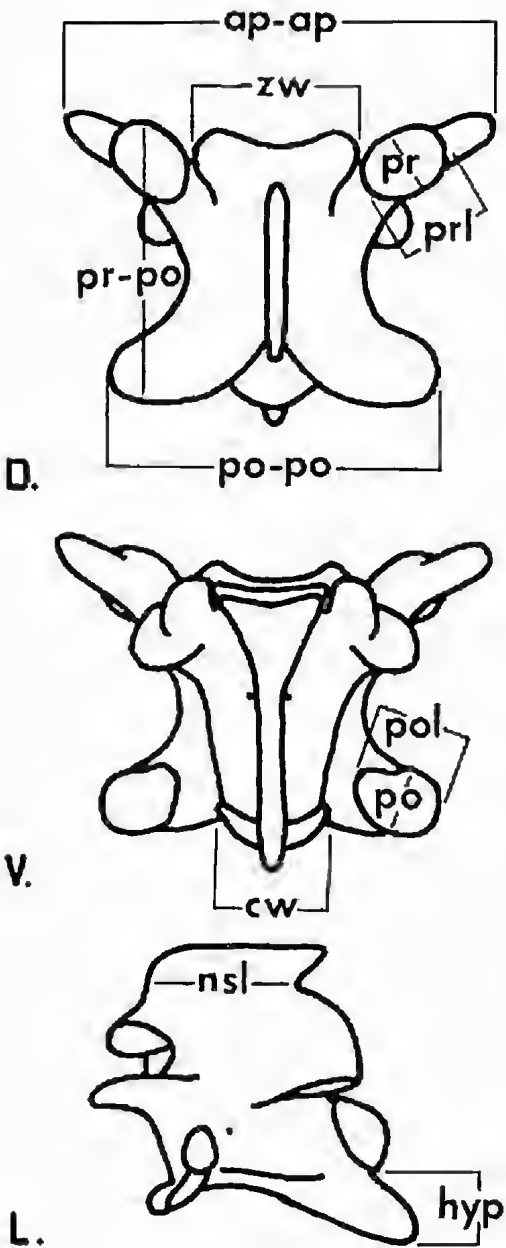


Fig. 1. Dorsal (D), ventral (V) and lateral (L) views of an elapid vertebra showing where measurements were taken.

- pol Length of postzygapophysis—the longest diameter of the postzygapophysial facet (even though this was almost perpendicular to the long axis of the centrum).
- po Width of postzygapophysis—the maximum diameter at right angles to the length.

- nsl Minimum length of neural spine—this usually occurred about halfway up the spine, as the dorsal edge overhangs posteriorly and/or anteriorly.
- zw Width of zygosphenes—the maximum width of the tenon.
- cw Width of condyle—the maximum diameter in the transverse plane.
- hyp Length of hypapophysis—the vertical distance from the lower edge of the condyle to the tip of the hypapophysis.

Results

The vertebrae conform with the general descriptions of Auffenberg (1963), Hoffstetter & Gasc (1969) and Johnson (1956).

***Pseudechis porphyriacus* (Shaw)**

The number of preloacal vertebrae (Table 1) is consistent with the number of ventral scales (184, according to Worrell 1963).

In every preloacal vertebra, the width across postzygapophyses exceeds the length between zygapophyses (Fig. 2). The hypapophysis arises near the lip of the cotyle, extends as a low lamella for about two-thirds the length of the centrum and then deepens sharply before tapering to a sharp point which does not much exceed the posterior surface of the condyle in any but the most anterior vertebrae. The hypapophyses of the anterior vertebrae are very long; they decrease in length fairly uniformly along the column (Fig. 2). The subcentral ridges are low and rounded. The dorsal articular facet of the paradiapophysis projects as a little round dome; the lower facet is saddleshaped. The prominent parapophysial processes are rounded anteriorly. They do not extend closer to the midline than the most lateral lip of the cotyle. Interzygapophysial ridges are faintly distinguishable. The neural spine is a low, laterally-compressed blade, its dorsal edge parallel with the long axis of the vertebra, its anterior edge almost vertical and its posterior edge overhanging.

The minimum length of the neural spine is about half the length between the zygapophyses [\bar{x} 0.53 \pm .0056 (35); \bar{x} 0.55 \pm .0049 (36)] (Fig. 3). The neural arch is slightly wider than high. The neural arches of most of the vertebrae do not extend backwards to form epizygapophysial spines, but such spines are well developed on the first five vertebrae and are distinguishable on the sixth to tenth. The cotyles and condyles are nearly round, but are slightly flattened dorsoventrally. The width of the condyle is about one third of the length

TABLE 1
 Total length, snout-to-vent length and number of vertebrae of specimens of four species of elapids

Species	SAM register number	Sex	Total length (mm)	Snout-vent length (mm)	Number of vertebrae			
					Pre-cloacal*	Cloacal	Post-cloacal	Total*
<i>Pseudechis porphyriacus</i>	R14060	no data	1220	no data	181	8	>42	>231
	R14061	no data	1375	no data	182	6	52	240
	R14062	no data	1120	no data	182	5	>30	>217
	R14063	no data	1070	890	177	5	48	231
<i>Austrelaps superba</i>	R14066	♀	515	433	143	4	42	189
<i>Notechis scutatus</i>	R14058	♂	930	775	174	5	58	237
	R14059	no data	no data	800	178	5	52	235
<i>Pseudonaja nuchalis</i>	R14064	♂	1555	1300	204	6	60	270
	R14065	no data	1100	910	206	5	52	273

* Atlas-axis complex not included in this count.

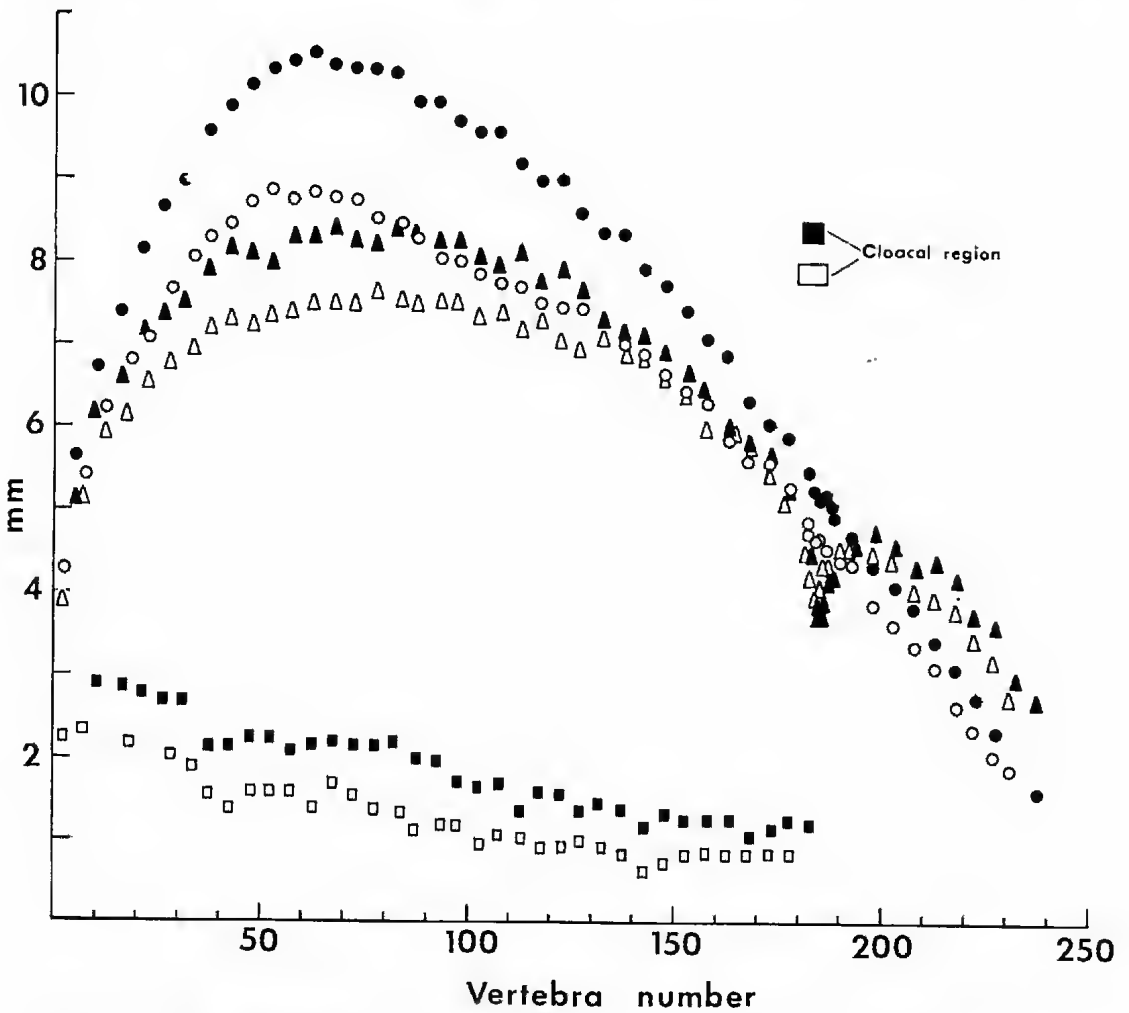


Fig. 2. Variation throughout the vertebral column in (a) length between zygapophyses (Δ \blacktriangle), (b) width across postzygapophyses (\circ \bullet) and (c) length of hypapophysis (\square \blacksquare) of two specimens of *Pseudechis porphyriacus*. Hollow symbols R14060, solid symbols R14061.

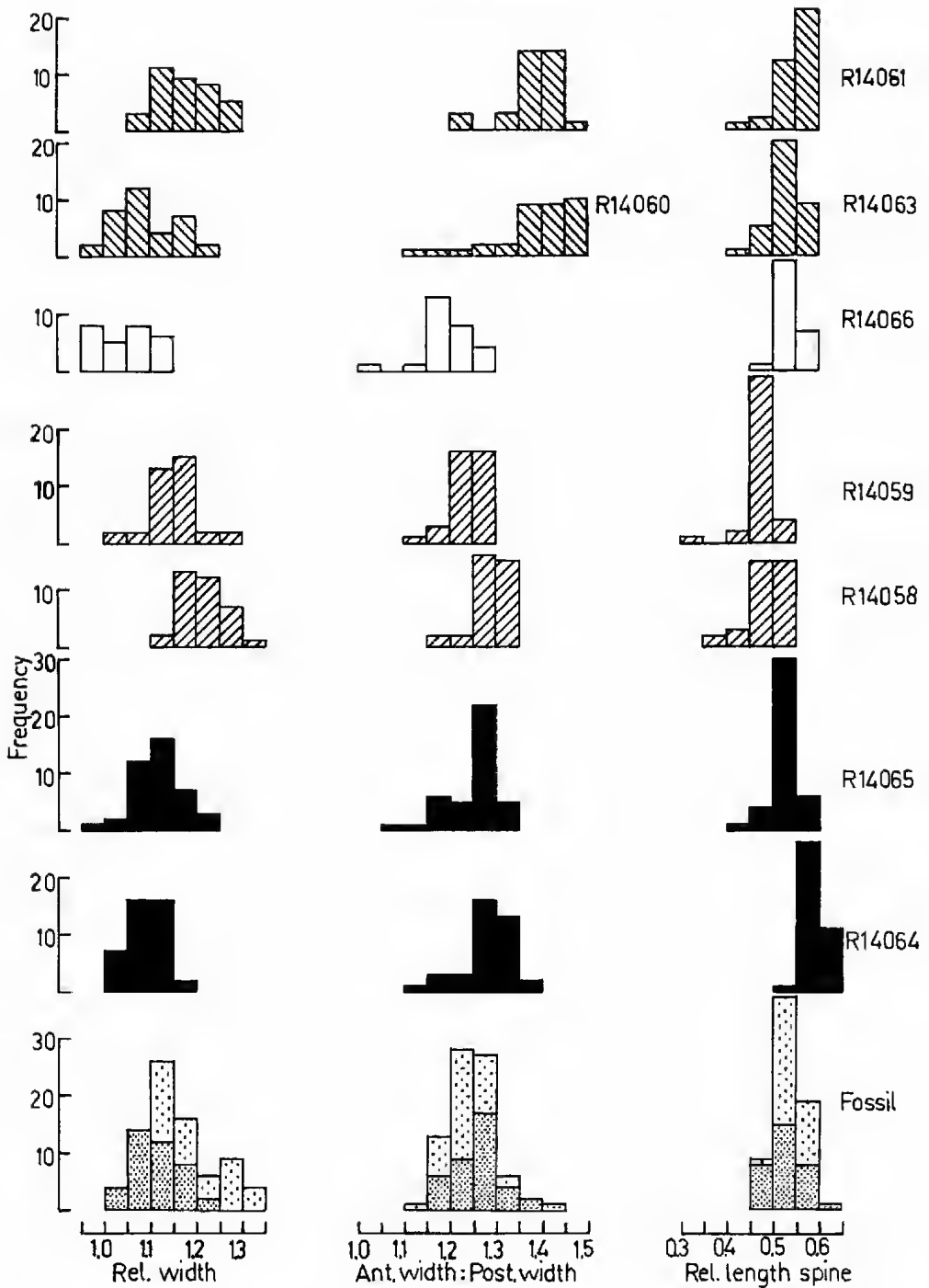


Fig. 3. Distributions of values for the ratios (a) width across postzygapophyses to length between zygapophyses, (b) width across accessory processes to width across postzygapophyses, and (c) minimum length of neural spine to length between zygapophyses. Left-to-right downward hatching, *Pseudechis porphyriacus*; open columns, *Austrelaps superba*; right-to-left downward hatching, *Notechis scutatus*; solid columns, *Pseudonaja nuchalis*; fine stipple, Victoria Cave, type A; coarse stipple, Victoria Cave, type B.

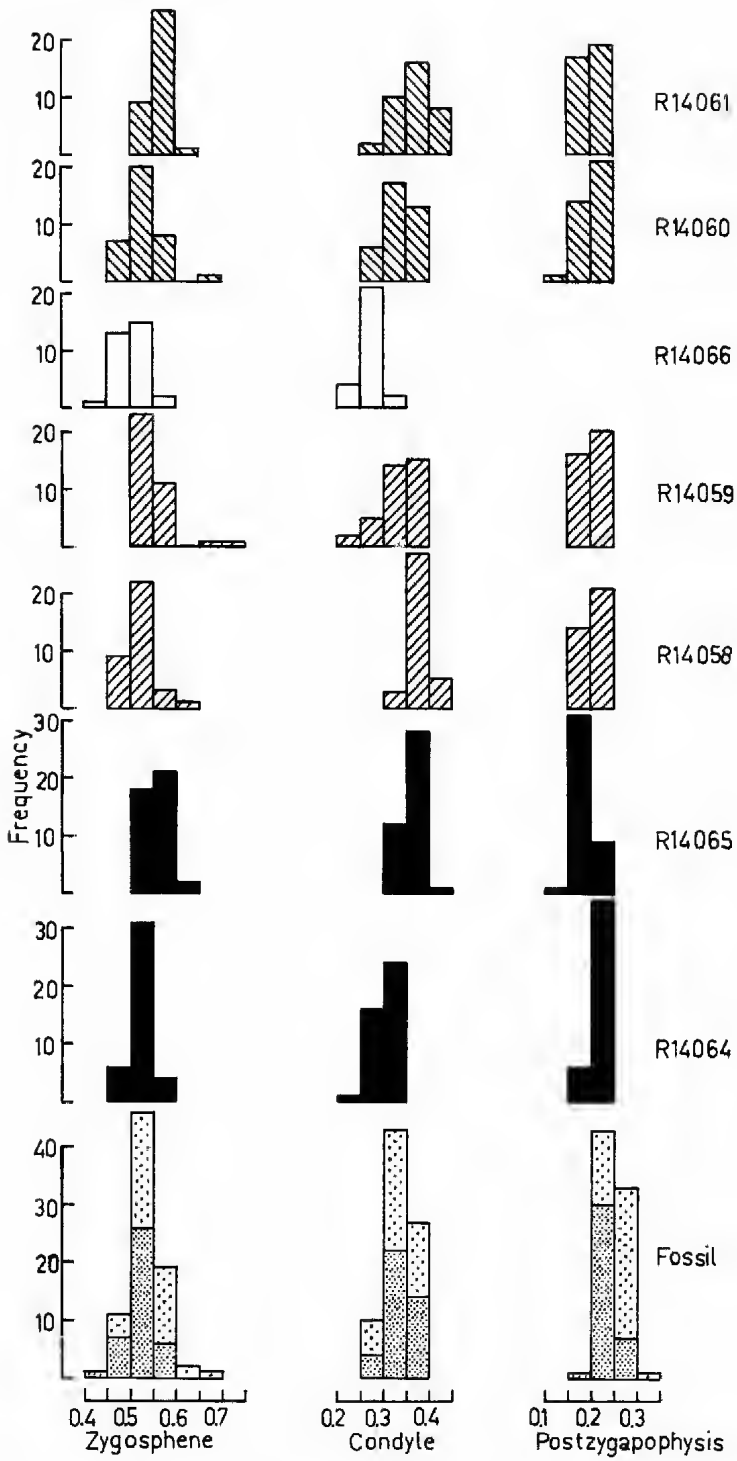


Fig. 4. Distributions of values for the ratios (a) width of zygosphere to length between zygapophyses, (b) width of condyle to length between zygapophyses, and (c) width of postzygapophysis to length between zygapophyses. Hatching as in Fig. 3.

TABLE 2

Some characteristics of the cloacal region of four specimens of *Pseustes porphyriacus*

Specimen	Total number of cloacal vertebrae	Number with articulated ribs	Number with single hypapophysis	Number with ribs deeply forked
R14060	8	1	2	8
R14061	5	1	3	5
R14062	5	4	4	4*
R14063	6	2	3	5*

* The anterior-most pair of ribs have shallow forks.

between zygapophyses [\bar{x} 0.33 \pm .0047 (36); \bar{x} 0.37 \pm .0067 (36)] (Fig. 4). The zygosphene, viewed from the front, is thin and straight or slightly convex; from above it is nearly straight or slightly concave with a faint median notch on some vertebrae. The width of the zygosphene is a little over half the length between the zygapophyses [\bar{x} 0.53 \pm .0063 (36); \bar{x} 0.57 \pm .0038 (35)]. The prezygapophysial facets are oblong [length/width 1.19–1.58, \bar{x} 1.40 \pm .019 (36); 1.01–1.73, \bar{x} 1.49 \pm .025 (36)]. The acute accessory processes extend laterally perpendicular to both vertical and horizontal axes of the vertebra, and project well beyond the articular facets. Hence the ratio of width across accessory processes to width across postzygapophyses is high [\bar{x} 1.39 \pm .014 (35); \bar{x} 1.38 \pm .010 (35)] (Fig. 3). The postzygapophyses are large [width postzygapophysis/length between zygapophyses: \bar{x} 0.20 \pm .003 (36); \bar{x} 0.20 \pm .002 (36)] and have an anterior notch that gives their otherwise ovate shape a kidney outline. The maximum diameter of the postzygapophysis is almost perpendicular to the long axis of the vertebra and exceeds the width [length/width 1.03–1.51, \bar{x} 1.27 \pm .020 (36); 1.02–1.46, \bar{x} 1.22 \pm .017 (36)].

The typical four pairs of foramina are present on all precloacal vertebrae, and in many vertebrae they are unilaterally or bilaterally doubled. For example, in the 183 precloacal vertebrae of R14061 the lateral foramina are bilaterally double (8 vertebrae), double on the right only (11) or left only (13); the paracotylar foramina are bilaterally double (1), double on the right only (5) or left only (8); the subcentral foramen is double on the right (2) or left (3) and in each of three vertebrae three pairs of subcentral foramina appear. A fifth pair of foramina is present in the precloacal vertebrae of all speci-

mens, each foramen of this pair opening through the accessory process near the anterolateral margin of the prezygapophysial facet.

Vertebral structure in the cloacal region varies widely between specimens, and the number of vertebrae with articulated forked ribs may be equal to or less than the number with a single hypapophysis (Table 2). The fork is deep on most forked ribs but on the most anterior cloacal vertebra, the notch may be midway along the rib. The lymphapophyses project laterally and slightly ventrally, as do the pleurapophyses of the post-cloacal vertebrae.

The haemapophyses of each post-cloacal vertebra arise separately from the ventral surface of the centrum, and remain completely separate, although on the anterior post-cloacal vertebrae the tips of the haemapophyses converge slightly. In lateral view the shape of the haemapophysis is similar to that of the hypapophyses of the precloacal vertebrae. The pleurapophyses are directed anterolaterally (viewed from above or below) and extend anterior to the cotyle.

Some irregularities occur in the skeletons. In R14060 the right prezygapophysial facets of the 130th to 134th vertebrae are enlarged to almost double the size of the left-side facet, and the right postzygapophyses of these vertebrae are slightly enlarged. A similar, but even greater, enlargement of the right prezygapophysis occurs in two vertebrae of R14062, where an outgrowth of spongy bone has completely fused the prezygapophysis to the preceding postzygapophysis, and the accessory process is reduced. These abnormalities probably resulted from injury, but R14063 shows slight congenital abnormalities, firstly on vertebra 91, where a small, but distinct epizygapophysial spine appears on the left side only, and secondly in four post-cloacal vertebrae. Near the beginning of the postcloacal series, the centra of two consecutive vertebrae are completely fused. On the left, the outline of the posterior edge of the neural arch of the first vertebra can be seen, but on the right the suture line is only faintly distinguishable. The pleurapophyses of both vertebrae lie close together, apparently fused to the centrum of the first vertebra. Two pairs of haemapophyses arise separately on the ventral surface of the combined centrum. Later in the post-cloacal series two vertebrae are more fully fused and share a common neural spine. Two pairs of haemapophyses are fused at their base near the condyle of the second vertebra. An apparently

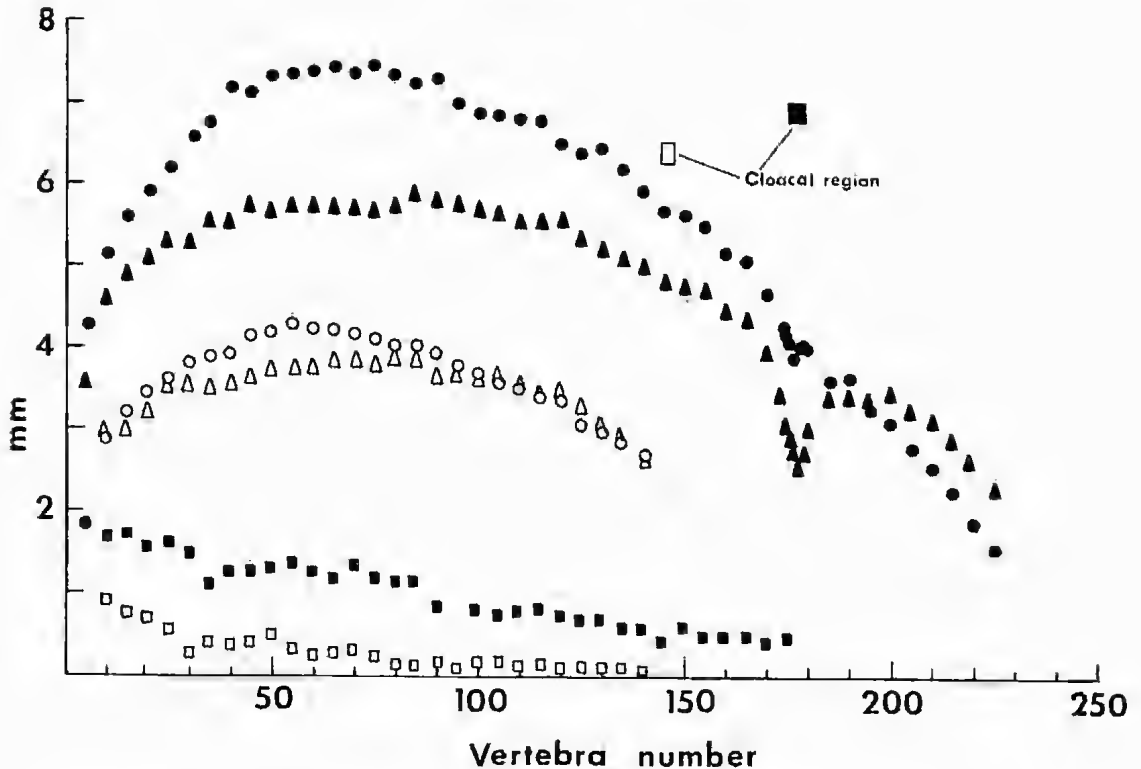


Fig. 5. Variation throughout the vertebral column in (a) length between zygapophyses (Δ \blacktriangle), (b) width across zygapophyses (\circ \bullet), and (c) length of hypapophysis (\square \blacksquare) in two species. Hollow symbols, *Austrelaps superba* (R14066), solid symbols, *Notechis scutatus* (R14058).

similar abnormality has been observed in dorsal vertebrae of colubrid snakes (King 1959).

Austrelaps superba (Günther)

The low number of precloacal vertebrae in this specimen (Table 1) is confirmed as typical of the species by the ventral scale number (151 according to Worrell 1963). The width across the postzygapophyses is less than the length between zygapophyses in the first ten and the last 35 precloacals (Fig. 3).

The hypapophysis (Fig. 5) is similar in form to that of *P. porphyriacus* and does not extend further posteriorly than the posterior surface of the condyle.

The subcentral ridges are low and rounded, as in *P. porphyriacus*, but the interzygapophysial ridges of *A. superba* are stronger. Small epizygapophysial spines occur on the first six vertebrae. The condyle is smaller, relative to the length between zygapophyses, than in *P. porphyriacus* (Fig. 4). The zygosphene is thin and slightly convex from the front, convex

from above. The ratio of zygosphene width to length between zygapophyses (Fig. 4) has a mean of $0.50 \pm .0038$ (27). The prezygapophysial facets are oblong, the postzygapophysial facets obovate. The acute accessory processes are relatively shorter than in *P. porphyriacus* in most vertebrae (Fig. 3).

Of the four cloacal vertebrae, one has articulated forked ribs and three have a hypapophysis. The haemapophyses of the post-cloacal vertebrae are long anteroposteriorly, about half the length of the centrum, and are completely double.

Notechis scutatus (Peters)

In all precloacal vertebrae, the width across the postzygapophyses exceeds the length between zygapophyses (Fig. 5). Each hypapophysis is extremely compressed laterally in a thin lamella that terminates posteriorly in a sharp point not extending posterior to the posterior surface of the condyle in any but the first 15 vertebrae, where the hypapophysis is

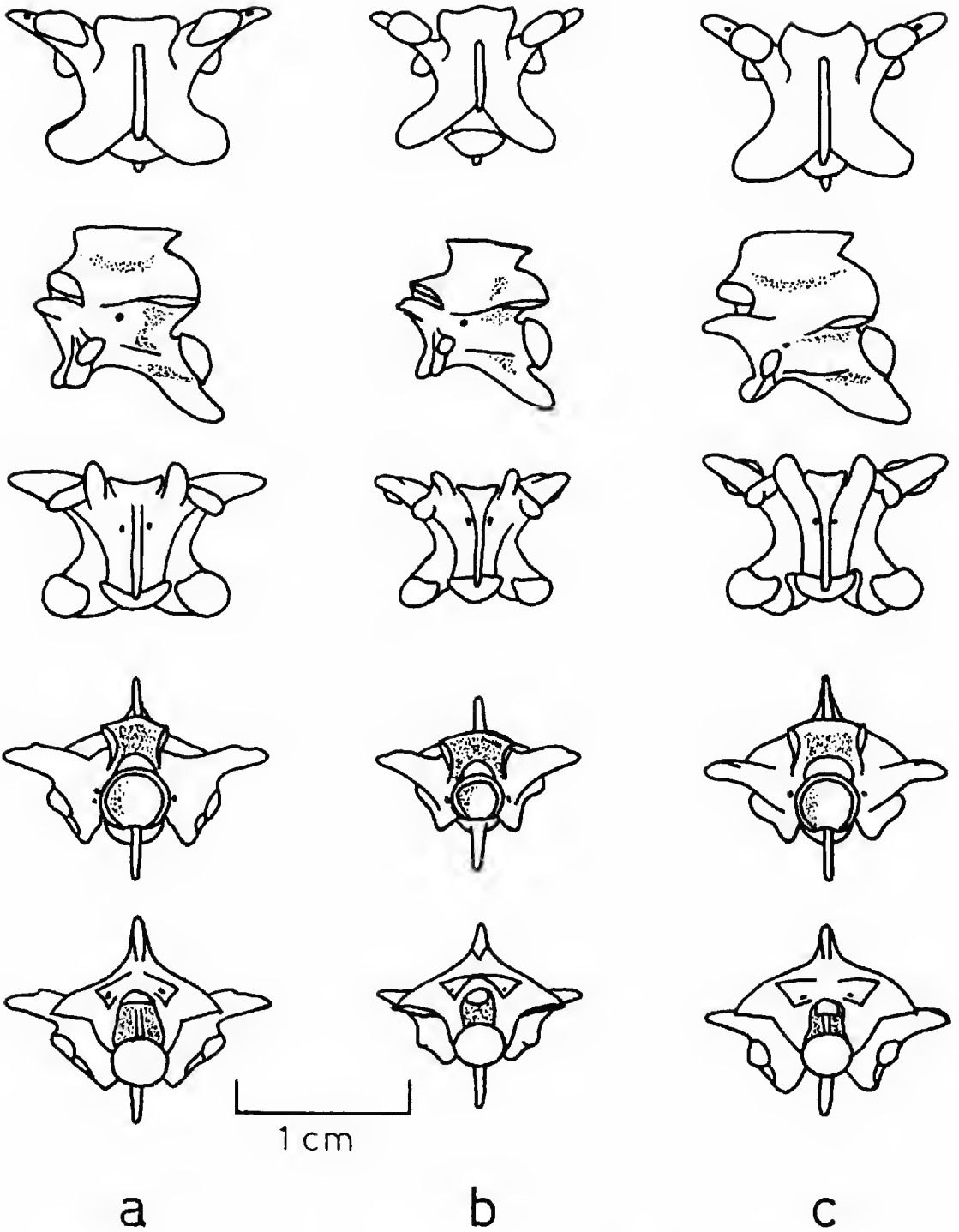


Fig. 6. Line drawings, to exact scale, of the 80th vertebra of (a) *Pseudechis porphyriacus* (R14060), (b) *Notechis scutatus* (R14059), and (c) *Pseudonaja nuchalis* (R14064) in dorsal, lateral, ventral, anterior and posterior views.

very long (Fig. 5). The subcentral ridges are low and rounded; the interzygapophysial ridges are weak but distinct. The neural spine is higher than in *P. porphyriacus* (Fig. 6) and its horizontal dorsal edge overhangs both anteriorly and posteriorly. The minimum length of the neural spine is generally relatively shorter than in the specimens of *P. porphyriacus* [ratio of minimum length of neural spine to length between zygapophyses: \bar{x} 0.48 \pm .0064 (35); \bar{x} 0.48 \pm .0049 (36)] (Fig. 3). Epizygapophysial spines are well developed on the first four vertebrae, faintly distinguishable on the fifth to eighth, but absent from all others.

The round condyle is set on a short but distinct neck (Fig. 6). The thin zygosphene is straight or slightly convex from the front, straight or slightly concave from above. The prezygapophysial facets are oblong [length/width 1.00–1.67, \bar{x} 1.47 \pm .027 (35); 1.09–1.58, \bar{x} 1.35 \pm .022 (35)]. The accessory processes are obtuse and short, so that the ratio of width across accessory processes to width across postzygapophyses is generally less than in *P. porphyriacus* (Fig. 3). The postzygapophyses are obovate [length/width 1.10–1.58, \bar{x} 1.35 \pm .021 (35); 1.00–1.47, \bar{x} 1.28 \pm .022 (35)], and their width is about one-fifth of the length between the zygapophyses (Fig. 4). Prezygapophysial foramina are constantly present.

In both specimens, all five cloacal vertebrae have fused forked ribs. One has three, the other two cloacal vertebrae with a single hypapophysis.

The haemapophyses are large, paddle-shaped and completely paired. The pleurapophyses extend ventrally more than laterally. The zygapophysial facets extend anteriorly and posteriorly, rather than laterally as in the pre-cloacal vertebrae, and acute accessory processes are distinct on all the postcloacal vertebrae.

Unilateral or bilateral doubling of the paracotylar and/or subcentral foramina occurs in a very few pre-cloacal vertebrae (no more than four in either specimen).

Pseudonaja nuchalis Günther

Pseudonaja nuchalis has more vertebrae than any of the other species studied here (Table 1), and maximum length and width occur in sequentially more posterior vertebrae than in the other species (Fig. 7). All pre-cloacal vertebrae are wider than long. The

hypapophysis is well developed on all pre-cloacal vertebrae. Thickenings on the rim of the cotyle on either side of the ventral midline give rise to a low ridge that narrows sharply to join the laterally-compressed hypapophysis. The hypapophysis deepens from about the middle of the vertebra and terminates in a rounded point that extends posteriorly to the condyle. Subcentral ridges are strong and interzygapophysial ridges are distinct. The paradiapophyses are well developed, with a protruding, dorsoventrally-elongated upper facet and saddle-shaped lower facet. The parapophysial processes appear in ventral view as a flat surface nearly as broad as long; the ventral projection of these processes is medial to the lateral border of the cotyle. The neural spine is low and long (Figs 3 and 6); its dorsal edge overhangs slightly at the front, markedly behind. Epizygapophysial spines are distinct on the first five vertebrae, faintly visible on the sixth to eighth and absent from all others. The cotyles and condyles are almost round; in R14065 some cotyles are depressed slightly, but in R14064 some are slightly compressed laterally. The condyles are relatively much larger in the smaller specimen than in the larger one (Fig. 4). The zygosphene is convex from the front, concave from above; it is thin in vertebrae of the smaller specimen but is thickened in those of the larger. The prezygapophysial facets are oblong [length/width 1.09–1.72, \bar{x} 1.39 \pm .022 (41); 1.18–1.78, \bar{x} 1.35 \pm .018 (41)], and the acute accessory processes extend laterally well beyond the articular facets (Fig. 3). Except for a slight notch posteriorly, the outline of the postzygapophysial facet is almost round [length/width 1.03–1.35, \bar{x} 1.17 \pm .011 (41); 1.09–1.59, \bar{x} 1.30 \pm .019 (41)].

In the cloacal region the ribs are all fused except for the anterior vertebra of R14064, and a hypapophysis occurs on one (R14065) or three (R14064) cloacal vertebrae.

The haemapophyses are completely paired and extend anteriorly as two separate ridges to the rim of the cotyle. The pleurapophyses are broad and flat and not pointed. In anterior view they project ventrolaterally but in ventral view mainly laterally and only slightly anteriorly.

In R14065, more than the one pair of paracotylar foramina appear on many vertebrae—15 pre-cloacal vertebrae have an extra paracotylar foramen on the right side, 18 on the left and 34 on both sides. R14064 has only

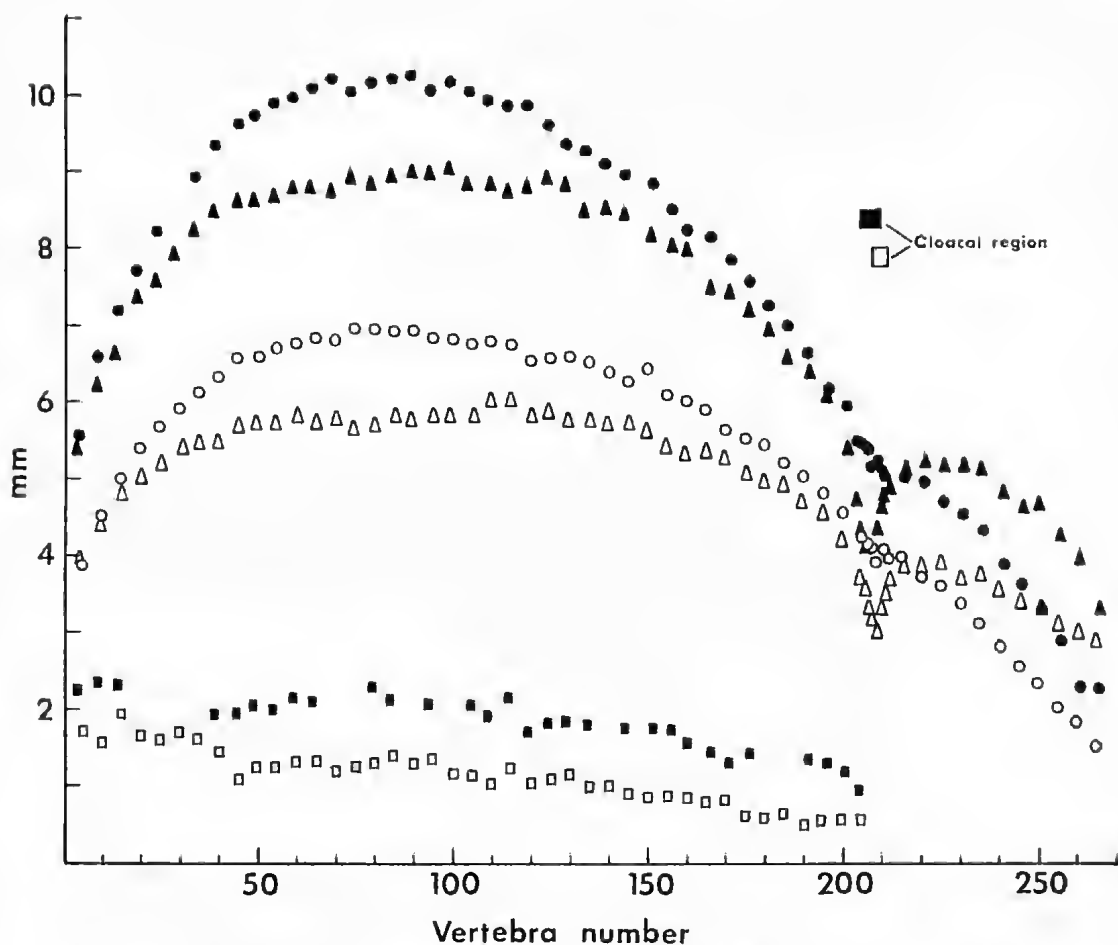


Fig. 7. Variation throughout the vertebral column in (a) length between zygapophyses ($\Delta \blacktriangle$), (b) width across zygapophyses ($\circ \bullet$), and (c) length of hypapophysis ($\square \blacksquare$) in *Pseudonaja nuchalis*. Solid symbols, R14064, hollow symbols, R14065.

8 precloacal vertebrae with additional paracotylar foramina. The left postzygapophysis of the 114th vertebra is fused by an outgrowth of spongy bone to the prezygapophysis of the succeeding vertebra, which lacks an accessory process on the left side. The left rib of vertebra 114 shows a healed fracture near the articulation with the vertebra.

Pleistocene fossil vertebrae from Victoria Cave

The precloacal vertebrae found in the Victoria Cave deposit vary in length from about 2 mm to a maximum length between zygapophyses of 11.1 mm. In their general conformation they closely resemble those of *Pseudonaja*. However within the sample of vertebrae from Victoria Cave, two types can be distinguished on the characteristics of the zygosphene: Type A; slightly convex when viewed from above,

convex in anterior view and slightly thickened; Type B: almost straight, with a median notch, when viewed from above, almost straight in anterior view and extremely thickened. This thickening is consistent with the robust appearance of the vertebrae. The subcentral ridges are particularly strong (Fig. 8).

As well as the thickening of the zygosphene, its width relative to the length between zygapophyses differs significantly between the types A and B [A, \bar{x} 0.52 \pm .0048 (40); B, \bar{x} 0.54 \pm .0057 (40); .002 < P < .01]. The distributions of the values for this ratio overlap widely not only between types A and B from Victoria Cave but also among the specimens studied (Fig. 4). The ratio of width across postzygapophyses to length between zygapophyses tends to be greater in the fossil vertebrae than in *A. superba*; the ratio of width

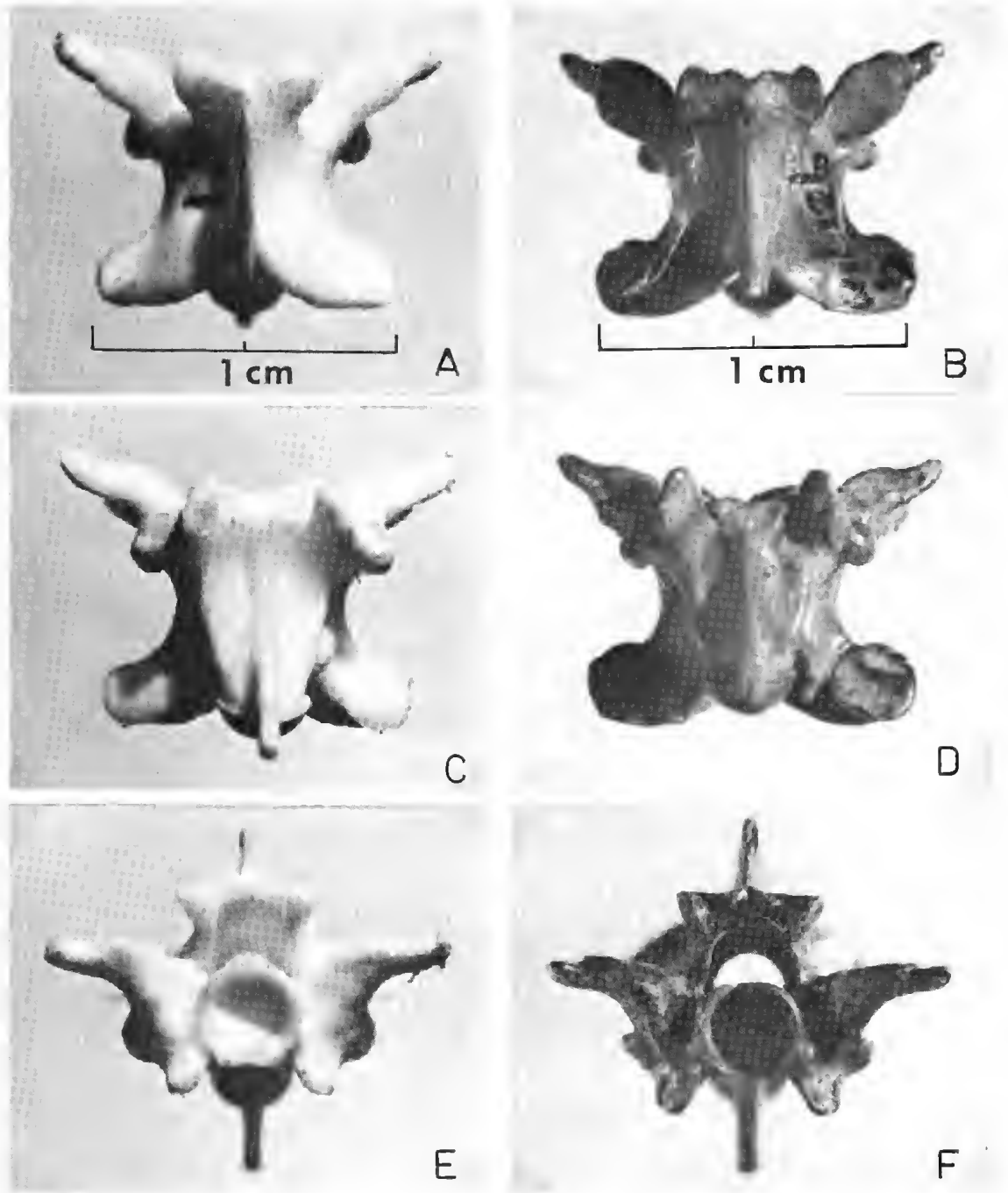


Fig. 8. Preloacal vertebrae of *Pseudonaja nuchalis*; left, 80th preloacal of R14064; right, Victoria Cave, Type B (P16126b) in dorsal (A, B), ventral (C, D) and anterior (E, F) views.

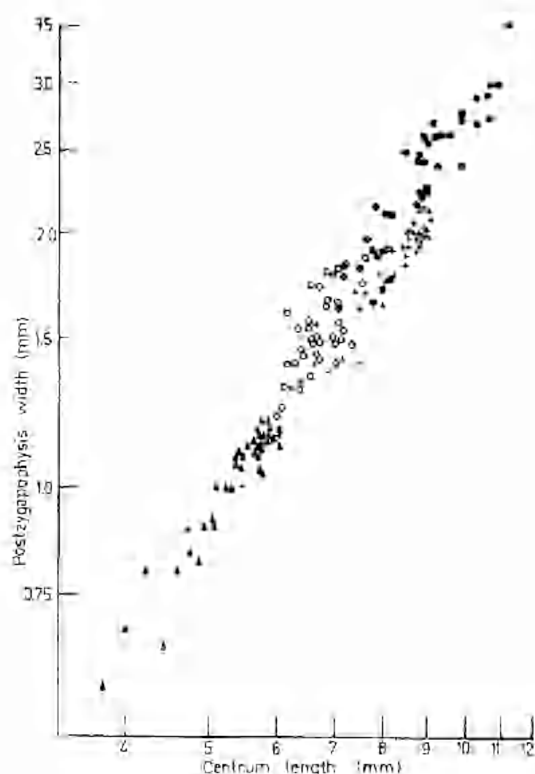


Fig. 9. Double-logarithmic regression of width of postzygapophysis on length between postzygapophyses in *Pseudonaja nuchalis*, \blacktriangle , R14054; $+$, R14064; \circ , fossil, Type A; \bullet , fossil, Type B.

across accessory processes to width across postzygapophyses is less than in most *P. porphyriacus* and the relative length of the neural spine is generally greater than in *N. scutatus* (Fig. 3). In these ratios, the Victoria Cave vertebrae closely resemble *P. nuchalis*. In the relative width of the condyle, the distribution of ratios for Victoria Cave vertebrae resembles the larger *P. nuchalis* (R14064), though not the smaller (R14065). Finally, in the relative width of the postzygapophyses the Victoria Cave vertebrae of Type A resemble the larger but not the smaller *P. nuchalis*, and the relative width of the postzygapophysis is generally greater in Type B fossils than in any of the modern species studied (Fig. 4).

This subjective and objective analysis of the fossil vertebrae indicates that they most closely resemble *Pseudonaja*. The Type A vertebrae can be referred with confidence to this genus. Because the Type B vertebrae differ in the thick zygosphenes and the relatively large post-

zygapophyses, the possibility exists that they are of a species different from Type A. However, these characteristics are two which develop with age (Luffenberg 1963) and most of the Type B vertebrae are larger than the Type A (Type A, length 6.0–8.1, \bar{x} 6.7; Type B, 7.1–11.1, \bar{x} 8.9) and also generally are larger than the vertebrae of the modern specimens. When the correlation between length between zygapophyses and relative width of postzygapophyses of Type B vertebrae was tested by the Kendall Rank Correlation Test (Siegel 1956) the correlation was found to be highly significant ($\tau = 0.41$, $z = 3.765$, $P < .001$). On a double-logarithmic plot of postzygapophysis width against length between zygapophyses, the distribution of values for the fossil vertebrae (of both types, A and B) falls near the same straight line as those of R14064 and R14065 (Fig. 9). The similarities between Victoria Cave preloacal vertebrae and those of modern *P. nuchalis* so far outweigh the slight differences that recognition of the fossils as a separate species seems unnecessary at least until the limits of variations of modern species are better known.

The post-cloacal vertebrae recovered from Victoria Cave resemble those of *P. nuchalis* in the laterally-directed pleurapophyses. In the other species studied the pleurapophyses project anterolaterally.

Discussion

In all the vertebrae of the four species, the hypapophysis is well-developed (as in all elapids) and hypapophysis length decreases slowly from anterior to posterior along the column. There is no suggestion of two distinct regions as in *Achrochordus javanicus* where the anterior region (to vertebra 96) has hypapophyses long and fairly constant in length and the posterior region has hypapophyses short and of constant length (Hoffstetter & Gayard 1964).

At family level, the presence of vertebral foramina may have diagnostic value [e.g. the constant absence of lateral foramina in *Achrochordidae* (Hoffstetter & Gayard 1964)], but the variability in the number of foramina at each position (i.e. lateral, subcentral, etc.) in the one snake indicates the need for caution in the use of foramina in taxonomy.

Although middle precaudal vertebrae may be the most constant in their structure (within species) and hence best for identification

(Auffenberg 1963), the difficulty of assigning an isolated elapid vertebra to a particular region of the column precludes confidence in selecting middle precaudals from a sample of fossils. Because of the consistent variations along the column, together with some irregular variation (e.g. doubling of foramina), to identify isolated vertebrae it is necessary to consider not just the middle precaudal vertebrae of reference specimens, nor the mean of some value (even if it be given with standard error) but the range through which a given character varies. Also because of variations along the column, no unique specific character was found, and so it is necessary to consider several characters in the identification of fossils. The

fossil genera may be readily identified, but further studies of congeneric species are needed to determine whether specific identification is possible.

Acknowledgments

Mr R. Shine, Mr G. Whitten and Dr R. T. Wells kindly donated the modern snakes. Dr Wells and members of the Cave Exploration Group of South Australia helped in excavating the fossil vertebrae. I am grateful to Dr R. T. Wells, Mr I. M. Thomas, Dr T. F. Houston and Mr N. Pledge for their criticisms of the manuscript. Mr P. Kempster prepared the photographs for Fig. 8.

References

- AUFFENBERG, W. (1963).—The fossil snakes of Florida. *Tulane Stud. Zool.* **10**, 131-216.
- HOFFSTETTER, R., & GASC, J. P. (1969).—Vertebrae and ribs of modern reptiles. In C. Gans (Ed.) "Biology of the Reptilia". Vol. 1, pp. 201-310.
- HOFFSTETTER, R., & GAYRARD, Y. (1964).—Observations sur l'osteologie et la classification des Achrochordidae (Serpentes). *Bull. Mus. natn. Hist. nat., Paris* (2), **36**, 677-696.
- JOHNSON, R. G. (1955).—The adaptive and phylogenetic significance of the vertebral form in snakes. *Evolution* **9**, 367-388.
- JOHNSON, R. G. (1956).—The origin and evolution of the venomous snakes. *Evolution* **10**, 56-65.
- KING, W. (1959).—Vertebra duplication, an osteological anomaly widespread in snakes. *Herpetologica* **15**, 87-88.
- LONGMAN, H. A. (1925).—Ophidian vertebrae from cave deposits at Marmor Quarry. *Mem. Qld Mus.* **8**, 111-112.
- LYDEKKER, R. (1888).—"Catalogue of Fossil Reptiles and Amphibians in the British Museum of Natural History." Part I. (London.)
- MCDOWELL, S. B. with a letter by H. Cogger (1967).—*Aspidomorphus*, a genus of New Guinea snakes of the family Elapidae, with notes on related genera. *J. Zool., Lond.* **151**, 497-543.
- MCDOWELL, S. B. (1970).—On the status and relationship of the Solomon Island elapid snakes. *J. Zool., Lond.* **161**, 145-190.
- MERRILEES, D. (1968).—Man the destroyer: late Quaternary changes in the Australian marsupial fauna. *J.R. Soc. W. Aust.* **51**, 1-24.
- RAWLINSON, P. A. (1969).—The reptiles of east Gippsland. *Proc. R. Soc. Vict.* **82**, 113-128.
- SIEGEL, S. (1956).—"Nonparametric statistics for the behavioural sciences." (McGraw-Hill: New York.)
- STORR, G. M. (1964).—Some aspects of the geography of Australian reptiles. *Senck. biol.* **45**, 577-589.
- WORRELL, E. (1963).—"Reptiles of Australia." (Angus and Robertson: Sydney.)